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The Kinetics of Amiben Absorption and Metabolism as Related to Species Sensitivity[1]

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Abstract. The rates of absorption and metabolism of 3-amino-2,5-dichlorobenzoic acid (amiben) were investigated in 3-day-old roots of amiben-sensitive velvetleaf (*Abutilon theophrasti* Medic.) and amiben-tolerant morningglory [*Ipomoea hederacea* (L.) Jacq.].

The initial rates of amiben absorption and binding were identically concentration dependent for both species for external concentrations from 0.02 to 500 mg/liter.

The rates at which the absorbed amiben was: 1) bound; 2) incorporated into an unidentified amiben complex (amiben-X) and *N*-(3-carboxy-2,5-dichlorophenyl)-glucosylamine (*N*-glucosyl amiben); and 3) accumulated in these tissues during a 24-hr period was investigated at widely different concentrations for both species. There were no salient differences between the species in their amiben absorption rate at 5 mg/liter, but the absorbed amiben was complexed as *N*-glucosyl amiben more rapidly and to a greater extent in morningglory; maximum rate of glucosylation was attained earlier after exposure to amiben in morningglory than in velvetleaf. At nearly equitoxic concentrations (100 and 1 mg/l, 5 and 0.05 mg/l for morningglory and velvetleaf, respectively), the rates at which the absorbed amiben was distributed among *N*-glucosyl amiben, amiben-X and amiben were very similar for both species, although morningglory absorbed amiben at the faster rate. At amiben concentrations required for equal expression of the herbicidal effect, morningglory conjugates amiben at a faster rate and tolerates higher levels of free amiben than velvetleaf. Amiben toxicity in a species is expressed at that concentration which saturates the glucosylation process, and results in amiben accumulation at sufficiently high levels to exert its toxic effect. A scheme for amiben metabolism in plants is presented.

The herbicide 3-amino-2,5-dichlorobenzoic acid (amiben) is widely used for the control of annual weeds by preemergence application in fields of soybeans. Morningglory (*Ipomoea* spp.) is one of the major troublesome weeds in soybeans (15). Amiben does not selectively kill morningglory because both weed and crop are almost equally tolerant to the herbicide (10).

The metabolism of this compound has been investigated for several species which are either tolerant or susceptible to amiben (1, 2, 3, 4, 5, 6, 10, 11), but the basis for plant sensitivity is not clear. Most of the amiben absorbed by both tolerant and susceptible plants is converted to *N*-(3-carboxy-2,5-dichlorophenyl)-glucosylamine (*N*-glucosyl amiben) (3, 4, 6, 10, 11). A smaller proportion is converted to an unidentified amiben complex (amiben-X) and an insoluble residue, both of which yield amiben when hydrolyzed by acid (10). In seedling tissues of several species, more than 90% of the radioactivity from ^{14}C-amiben absorbed in 24 hr could be accounted for in the amiben moiety (10). The amount of *N*-glucosyl amiben in a soybean plant remained nearly constant for 50 days after amiben treatment (11). Thus, amiben does not appear to be degraded to any appreciable extent in plants. Rather, it appears to be complexed or conjugated with natural plant products.

In 6 species exhibiting a wide range in tolerance to amiben, the distribution of plant absorbed amiben among *N*-glucosyl amiben, amiben-X, and free amiben 24 hr after exposure to 0.5 mg/l correlated with species sensitivity (10). As species sensitivity to amiben increased, larger proportions of the total amiben in the 3 compounds were present as amiben-X and amiben; concomitantly, the fraction present as *N*-glucosyl amiben decreased. In several species which were almost equally sensitive to amiben, the percent distribution of amiben among these 3 compounds was similar. The concentration of any of these compounds, however, was species dependent without regard to sensitivity. Although the distribution data which were obtained at a single amiben concentration after 24 hr of treatment correlated with species sensitivity, the rates of formation of these compounds as functions of amiben concentration and plant sensitivity are not known.

[1] Cooperative investigations of the Crops Research Division, Agricultural Research Service, United States Department of Agriculture and the University of Illinois Agricultural Experiment Station, Urbana, Illinois.

The purpose of this study was to investigate the kinetics of amiben absorption and metabolism in both tolerant and susceptible plants. Ivyleaf morningglory [*Ipomoea hederacea* (L.) Jacq.] and velvetleaf (*Abutilon theophrasti* Medic.) were used in the study, as these plants differ greatly in their amiben sensitivity. As indicated by the amiben concentration required to reduce radicle extension by 50 % in 3-day-old seedlings, morningglory is of the order of 100 times more tolerant to this herbicide than velvetleaf (10).

Materials and Methods

Herbicide. Carboxyl-labeled ^{14}C-amiben (1.1 mc/mmole) with or without technical amiben was dissolved in a small volume of methanol for tissue treatment. As treatment concentration increased, the radioactive form was used with increasing dilution with the non-labeled form. ^{14}C-amiben was used for treatments up to 1 mg/l, while dilutions with technical amiben up to 100 fold were used at 500 mg/l.

Plant Material. Morningglory and velvetleaf seeds were cleaned in 0.5 % hypochlorite and rinsed several times with tap water. The seeds were vacuum infiltrated for about 20 min in 10^{-4} M $CaCl_2$, then germinated in paper towels moistened with the same solution. After 3 days of growth at 25°, the roots were excised at the crown for treatment.

Tissue Treatment. Root tissues (0.2–0.5 g) were incubated in Erlenmeyer flasks in the dark at 30° in a shaking water bath. Each flask represented an experimental unit. At harvest, the tissues were rinsed for 1 min in tap water, surface dried, and weighed.

To determine the influence of amiben concentration on the initial rate of amiben absorption, tissues were incubated for 90 to 120 min in solutions containing amiben at 0.02 to 500 mg/l and 0.05 M citrate-phosphate buffer at pH 6.0. All treatments were repeated in triplicate.

For determining the rates of amiben metabolism, the tissues were incubated for periods up to 24 hr in solutions containing amiben and 1 % (w/v) sucrose. The treatments were not replicated but replicate experiments were conducted.

Extraction, Purification and Measurement of Amiben and its Metabolites. After harvest, the fresh root tissues were homogenized with a conical, ground-glass homogenizer in absolute methanol. The methanol-insoluble residue then precipitated at 0° for 16 to 24 hr. After heating to about 20°, the methanol-soluble portion was then decanted for analysis.

Total amiben was determined by radioactivity measurements of the homogenate. Methanol-soluble radioactivity was measured from samples of the supernatant, and methanol-insoluble amiben was calculated as the difference between the total and supernatant measurements.

The radioactivity associated with the methanol-insoluble fraction was taken as a measure of the "bound" amiben.

The methanol-soluble supernatant contained amiben, amiben-X, and *N*-glucosyl amiben. These compounds were purified, separated and measured by the method described previously (10). The methanol-soluble material was concentrated *in vacuo*, purified in Florisil[2], then reconcentrated *in vacuo*. Purified extracts were chromatographed on glass plates coated with silica gel G using isopropanol:ammonium hydroxide:water (8:1:1, v/v/v) as the solvent. The positions of the 3 amiben containing compounds were located under UV light on the developed plates by comparison with parallel standards. The R_F values for these compounds corresponded to those previously reported for this system (9, 12). For quantitation, the silica gel which contained each compound was removed from the developed plate for radioactive assay. From 95 to 100 % of the purified-extract radioactivity which had been applied to the plate could be recovered from the 3 spots. The tissue concentration of each compound was calculated from the distribution of radioactivity among the 3 chromatographic spots and the total methanol-soluble activity.

Radioactivity Assay. Radioactivity was measured by liquid scintillation spectrometry. The scintillation solution consisted of 4 g 2,5-diphenyloxazole, 50 mg 1,4-bis-[2(5-phenyloxazolyl)]-benzene, 50 g naphthalene, and 134 ml ethyleneglycolmonoethylether made to 1 liter with dioxane. One to 3 ml of the methanol homogenate or methanol-soluble material was mixed with 10 ml of the scintillation solution for counting. The silica gel from the thin-layer plates was counted in 10 ml of the solution. Counting efficiency was determined by the channels-ratio method.

Results

Initial Rates of Amiben Absorption. Absorption and binding rates were not tested for linearity at the various concentrations, but the following facts indicate that the rates were constant with time during the experimental period: 1) identical rates were observed for each concentration in separate experiments lasting 90 to 120 min, and 2) the binding and absorption rates were relatively linear for the several concentrations in the metabolism studies presented below. Also, solution amiben concentrations remained essentially constant as no more than 8 % of the available amiben was absorbed for any treatment.

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[2] Mention of a trademark name or a proprietary product does not constitute a guarantee or warranty of the product by the USDA or the University of Illinois, and does not imply its approval to the exclusion of other products that may be suitable.

The rates (v, μg amiben g^{-1} hr^{-1}) of total amiben absorption and amiben binding in both morningglory (tolerant) and velvetleaf (susceptible) roots could be expressed as a function of concentration (C, mg/l) over a wide range of concentrations by the equation,

$$\log v = n \log C + \log k \qquad (I)$$

where k and n are parameters. This expression for absorption has been used to express root affinities for several substances over a relatively wide range of concentrations in different species (13, 14). The parameter n has been interpreted to be a relative measure of the affinity of roots for a substance. Greatest root affinity is indicated by small values of n. Values for n are obtained by plotting log v against log C and n is the slope of the curve.

The initial rates for amiben absorption for each species conformed to equation I over the entire range of concentrations tested (Fig. 1, upper curve). However, there was no significant difference ($P = 0.01$) in slopes or intercepts of the calculated curves for each species. This indicated no species differences in amiben affinity (n). Therefore, the data were combined and a single curve for both species generated ($r^2 = 0.998$).

There was also no significant species difference ($P = 0.01$) between each of the calculated curves for the initial rates of amiben binding for external concentrations up to 50 mg/l, so these data were also pooled (Fig. 1, lower curve) to give a good straight-line fit ($r^2 = 0.988$). Above concentrations around 50 mg/l, the curve decreasingly departs from linearity, with no apparent differences between species. The bound portion constituted 43, 37, 34, 32, 19, and 11 percent of the total absorbed at 0.02, 1.0, 10, 50, 200, and 500 mg/l, respectively, for the 2 curves shown in Fig. 1.

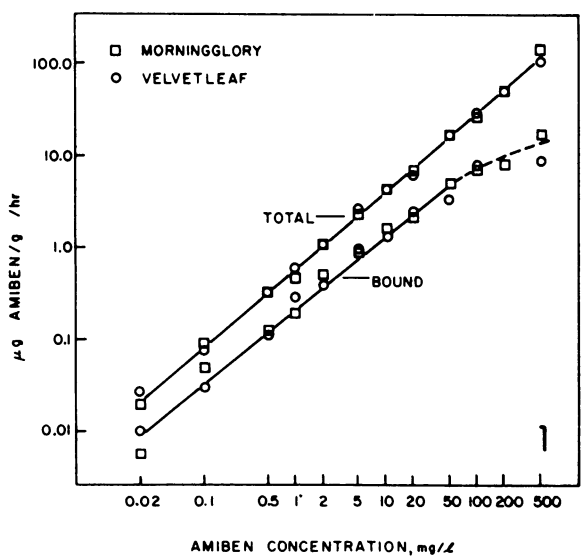


FIG. 1. Initial rates of amiben absorption and binding at various but constant amiben concentrations, based on the averages from 2 experiments. The upper curve represents the best straightline fit for total amiben absorption for both species. The lower curve represents the best straight-line fit of the insoluble absorption data for both species up to 50 mg/l; curve above 50 mg/l is a free hand extension. Equations log v = 0.853 log C — 0.221 and log v = 0.816 log C — 0.654 for upper and lower curves respectively, were determined by the method of least squares (8).

These data also indicated an identical concentration dependence for absorption and binding in both species.

Rates of Amiben Metabolism. Since a relative measure of the toxic effect of amiben (inhibition of radicle extension) was expressed to the same degree in both tolerant and susceptible plants at widely different concentrations (10), the kinetics of absorption and metabolism were investigated at several concentrations.

The herbicidal rate of amiben (2–3 lb/acre) would probably give a soil solution concentration on the order of 5 mg/l in the soil layer where seedlings develop. A concentration of this order can be derived by assuming uniform distribution of herbicide in the soil solution of a 6 inch layer of soil at 20% moisture. As measured by radicle elongation, a solution containing this amiben concentration is much more toxic to velvetleaf than to morningglory (10). When exposed to 5 mg/l, total amiben absorption proceeded linearly in both morningglory (Fig. 2) and velvetleaf (Fig. 3) for the 24-hr period. Amiben binding occurred at a near-linear rate in both species, but the amount bound was a small portion of total absorbed. Insignificant species differences in the rates of total amiben absorption and binding for 15 hr were evident from the data. *N*-glucosyl amiben synthesis lagged initially in both tissues, then proceeded much more rapidly in morningglory than in velvetleaf. Concomitant amiben accumulation and amiben-X synthesis, however, proceeded at the most rapid rates in velvetleaf. The maximum rate of glucosylation occurred sooner after exposure to amiben in morningglory than in velvetleaf. Most of the amiben absorbed by morningglory was complexed as *N*-glucosyl amiben. In contrast, free amiben accumulated to a higher level than any other component in velvetleaf.

Since species sensitivity correlated with the amiben distributed among the 3 methanol-soluble components after a 24-hr treatment (10), it also was of interest to observe these rates of distribution throughout the 24-hr absorption period. At 5 mg/l, the proportion of the amiben in the methanol-fraction which was complexed as *N*-glucosyl amiben increased more rapidly and leveled off at a much higher level in morningglory (Fig. 4) than in velvetleaf (Fig. 5). The fraction present as unaltered amiben was high initially in both species, but the proportion present after initial absorption was highest in velvetleaf. Amiben-X remained proportionately lower throughout the experiment in morningglory than in velvetleaf. After an initial period of about 8 to 10 hr,

during which the proportion of the 3 constituents changed appreciably in both species, there ensued an apparent steady state where the absorbed amiben was distributed among the components in a rather constant proportion.

Amiben concentrations of about 100 and 1 mg/l are required to inhibit radicle extension by 50 % in morningglory and velvetleaf, respectively (10). The kinetic data for the tissues treated at these nearly equitoxic concentrations revealed that the rates of amiben absorption and binding were linear in both plants, but occurred almost 100-fold faster in morningglory (Fig. 6) than in velvetleaf (Fig. 7). Moreover, the rates of accumulation and synthesis of the 3 methanol-soluble constituents were also greater in morningglory. Relative to the total amount of amiben absorbed into the methanol-soluble phase, the rates of accumulation and synthesis of these components was similar in both species. This can be clearly seen from the similarity in the time course of distribution among the 3 constituents (Fig. 8). Compared to the 5 mg/l treatment, morningglory produced proportionately less *N*-glucosyl amiben, but more amiben-X; the fraction of amiben present is also greater. These data compare favorably with those obtained for velvetleaf at 5 mg/l, except that there appears to be proportionately more *N*-glucosyl amiben but less amiben and amiben-X at 1 mg/l.

Five mg/l is about one-twentieth the concentration required to inhibit radicle extension 50 % in morningglory (10); the parallel concentration for velvetleaf is about 0.05 mg/l.

In velvetleaf roots which were treated with 0.05 mg/l amiben, the rates of total absorption and binding were linear (Fig. 9), but slower than in these same tissues which were exposed to the higher concentrations (Fig. 3, 7). A greater portion of the absorbed amiben was bound at the lowest concentration. *N*-glucosyl amiben synthesis lagged initially, but this compound was the major component present later in the experiment (Fig. 9). Amiben accumulated to a high level initially, but the level declined after about 6 hr; this decline accompanied an increase in the rate of glucosylation. Synthesis of amiben-X proceeded at a slow rate throughout.

Comparison of the parallel treatments of 5 mg/l in morningglory (Fig. 2) and 0.05 mg/l in velvetleaf (Fig. 9) showed that the time lag required to attain the maximum rate of glucosylation was longer in velvetleaf. In addition, the distribution data for these treatments were not as similar (Fig. 4, 10) as it was for the equitoxic treatments of 1 and 100 mg/l (Fig. 8). The major species difference at the parallel and relatively nontoxic levels of 0.05 and 5 mg/l for the respective species was that the proportion of the methanol-soluble radioactivity complexed as *N*-glucosyl amiben increased at the slowest rate in velvetleaf (Fig. 10); but this proportion steadily increased and after 24 hr approached the apparent steady state distribution attained earlier by morningglory (Fig. 2).

In the above kinetic studies, essentially constant external amiben supply was indicated as less than 5 % of the available amiben was absorbed in any treatment.

Discussion

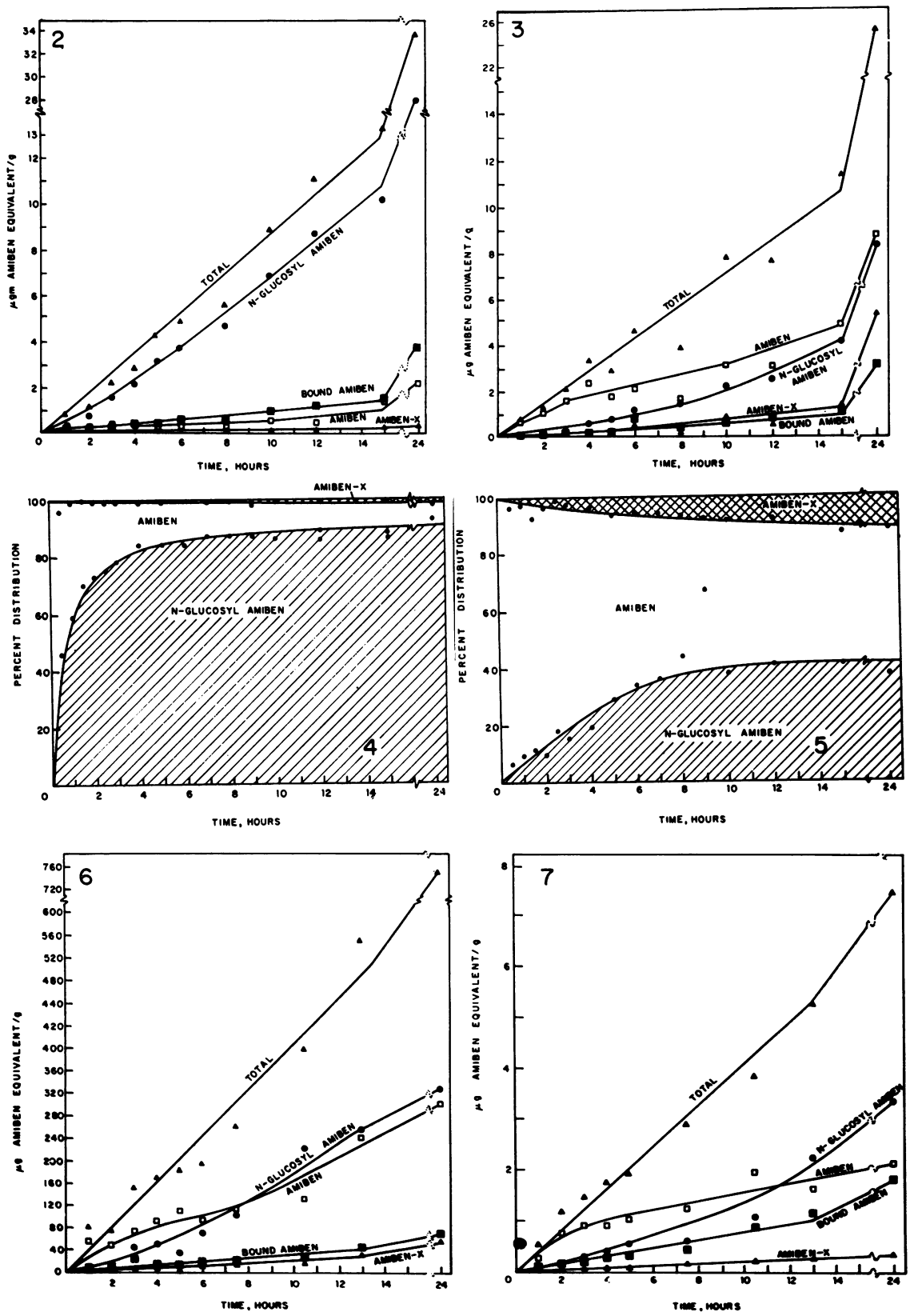
One purpose of subjecting the absorption data for each species to equation I was to test the possibility that plant sensitivity to amiben resulted from a difference between tolerant and susceptible plants in their apparent affinity for amiben. Utilizing the suggested interpretation for the biological significance of n (14), identical affinities of morningglory and velvetleaf roots for amiben were indicated. Thus, the differential sensitivity of these plants for amiben can be attributed to another factor.

Similarly, equal affinities for amiben binding were shown (Fig. 1). Departure from linearity of the amiben binding curve was interpreted to result from saturation of the binding capacity of the roots with amiben.

Based on the available data, a generalized scheme for the qualitative absorption and metabolism of amiben by plants for periods of at least 24 hr is proposed (Fig. 11). The reactions are numbered to facilitate discussion. Reversibility of all reactions is indicated, but there is evidence for reversibility of only certain reactions; several plant tissues treated with amiben-X contained all 3 of the methanol-soluble components and the incubation solution contained amiben (9). A boundary between plant and solution is shown.

Evidence for the qualitative existence of this general scheme is as follows. Incorporation of external amiben into either the soluble pool or the bound fraction involving reactions 1 and 2 (Fig. 11) was suggested by: 1) the near-linear rates of amiben incorporation for these processes at all concentrations tested (Fig. 2, 3, 6, 7, 9); 2) equal affinities of these plant processes for external amiben (up to concentrations which saturated the binding capacity) (Fig. 1); and 3) the initial rates of these processes were concentration dependent for a wide range of concentrations (Fig. 1). Amiben binding *via* the plant soluble pool is possible, but does not seem probable since the rate of binding was not associated with the internal concentration of any methanol-soluble components.

Further, plant amiben is apparently metabolized to *N*-glucosyl amiben or amiben-X by the indicated parallel reaction. For such a reaction the amount of amiben converted to each product is determined by the relative rates of each succeeding reaction (7). Higher levels of *N*-glucosyl amiben than amiben-X in all the experiments indicate that reaction 4 proceeds faster than reaction 3. In addition, greater proportions of amiben-X were produced in tissues treated with the more toxic levels of amiben than in those at less toxic levels. The major pathway for


2
µgm AMIBEN EQUIVALENT/g
TOTAL
N-GLUCOSYL AMIBEN
BOUND AMIBEN
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TIME, HOURS
3
µg AMIBEN EQUIVALENT/g
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AMIBEN
N-GLUCOSYL AMIBEN
AMIBEN-X
BOUND AMIBEN
TIME, HOURS
4
PERCENT DISTRIBUTION
AMIBEN-X
AMIBEN
N-GLUCOSYL AMIBEN
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µg AMIBEN EQUIVALENT/g
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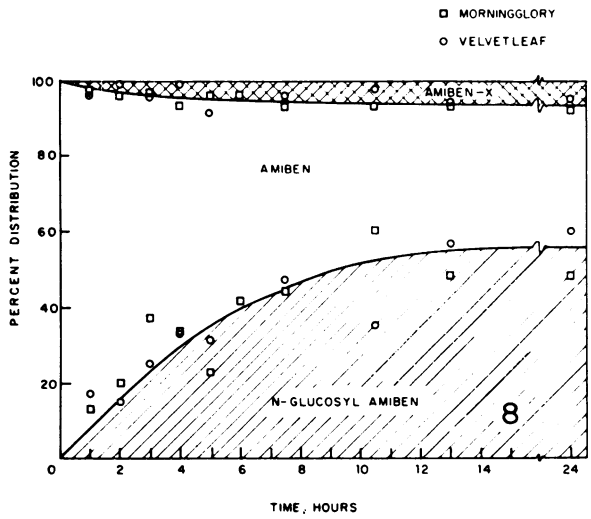

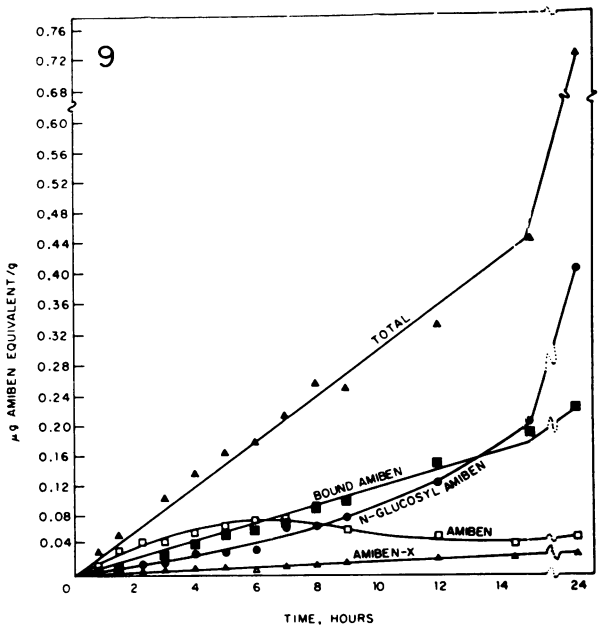

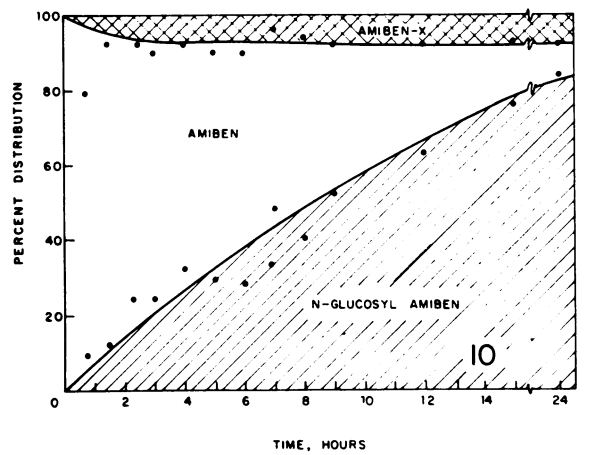

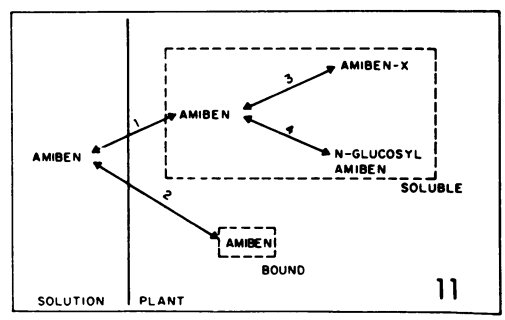

FIG. 2. The rate of amiben incorporation into the various components of morningglory roots at 5 mg/l amiben.

FIG. 3. The rate of amiben incorporation into the various components of velvetleaf roots at 5 mg/l amiben.

FIG. 4. The qualitative distribution of radioactivity with time among the three constituents in the methanol-soluble extracts of morningglory roots treated with 5 mg/l amiben.

FIG. 5. The qualitative distribution of radioactivity with time among the 3 constituents in the methanol-soluble extracts of velvetleaf roots treated with 5 mg/l amiben.

FIG. 6. The rate of incorporation into the various components of morningglory roots at 100 mg/l amiben.

FIG. 7. The rate of amiben incorporation into the various components of velvetleaf roots at 1 mg/l amiben.

FIG. 8. The qualitative distribution of radioactivity with time among the 3 constituents in the methanol-soluble extracts of morningglory and velvetleaf roots at equitoxic concentrations of amiben (100 mg/l for morningglory and 1 mg/l for velvetleaf).

FIG. 9. The rate of amiben incorporation into the various components of velvetleaf roots at 0.05 mg/l amiben.

FIG. 10. The qualitative distribution of radioactivity with time among the methanol-soluble constituents in velvetleaf roots treated with 0.05 mg/l amiben.

FIG. 11. A proposed scheme for amiben metabolism in plants.

amiben metabolism is *via* reaction 4, but can be converted to amiben-X when the glucosylation route becomes "saturated."

Species sensitivity is apparently a function of the amiben concentration required to saturate the glucosylation process. That concentration is lower in sensitive plants than in tolerant plants. When the rate of *N*-glucosyl amiben synthesis does not closely parallel the rate of absorption into the soluble pool, amiben accumulates and proportionately more amiben-X is produced. Presumably then, toxicity results when the level of amiben becomes sufficiently high to exert its toxic effect. This situation prevailed at the relatively toxic levels for both species [100 mg/l for morningglory (Fig. 6) and 5 and 1 mg/l for velvetleaf (Fig. 3, 7)]. Significantly, the concentration of amiben within the tissues required for equal expressions of toxicity was much higher in morningglory than in velvetleaf.

When the tissues were exposed to the relatively nontoxic levels [5 mg/l for morningglory (Fig. 2) and 0.05 mg/l for velvetleaf (Fig. 9)], glucosylation occurred at a sufficiently rapid rate to consume the accumulating amiben and lessen the diversion of amiben to amiben-X.

Because amiben-X levels were highest in those tissues exposed to the more toxic amiben concentrations in both morningglory and velvetleaf as well as in other species (10), speculating that amiben-X is a toxic product accounting for the herbicidal effect looks attractive. This is probably not the case, however, as amiben-X has been shown to be relatively non-phytotoxic (9).

The difference between species in the kinetics of amiben absorption and metabolism offers an explanation of the observed correlation of species sensitivity with the distribution of amiben among *N*-glucosyl amiben, amiben-X and amiben in 6 species treated with 0.5 mg/l amiben for 24 hr (10). Moreover, the data support the proposal that both *N*-glucosyl amiben and amiben-X are detoxication products of amiben (2, 3, 4, 9, 10, 11, 12), and fortify the contention that species sensitivity depends on the rate or extent of *N*-glucosyl amiben production (12).

The capacity for increasing the rate of *N*-glucosyl amiben synthesis after exposure to amiben could be attributed to the time required for activation or synthesis of the enzyme or other factors. Since the maximum rate of glucosylation was attained faster in morningglory than in velvetleaf, the high initial enzymatic activity for *N*-glucosyl amiben synthesis also offers a means for a plant to resist the toxic action of amiben. The capacity for glucoside synthesis, however, seems to be limited to a certain portion of the soluble pool, and is dependent on species sensitivity and the external concentrations (or the rate of amiben absorption).

Therefore, the bases for species sensitivity appear to be that the tolerant plant possesses the capacity to 1) sustain higher internal concentrations of free amiben for a parallel expression of the herbicidal effect and 2) conjugate the absorbed amiben more rapidly and to a greater extent than the susceptible plant. Both factors may be of equal importance in amiben sensitivity.

Species sensitivity is relative in that a toxic effect of amiben (inhibition of radicle elongation) is expressed to the same extent in tolerant or susceptible plants at the appropriate external concentration. The above experiments indicate that the rates of distribution among the methanol-soluble components nearly parallel this toxic expression. These facts might indicate that amiben kills all plants in the same way; only the concentration required differs.

Acknowledgments

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